GEOGRAPHIC RANGE AND INTRASPECIFIC VARIATION OF COULTER PINE

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In conjunction with a recent study of the natural hybrid between Coulter and Jeffrey pines, an analysis was made of the characters of several trees in each of nine populations throughout the range of Coulter pine (*Pinus Coulteri* Lamb.). These populations were chosen to include different geographical areas and elevational zones; it was found that they were isolated from each other, especially in the northern portion of the species range. The locations and elevations of the populations are listed in Table 1.

Coulter pine is generally regarded as a species endemic to California. It is found from Mount Diablo and Nortonville (Contra Costa County) in the north to a point in the vicinity of the Mexican border in the south. Some authors, Sudworth (1908) and Martinez (1945), state that Coulter pine is also found in the Sierra de San Pedro Martir, a mountain range in the northern part of Baja California, Mexico, but this has not been substantiated by other investigators (Wiggins, 1940, Duffield, personal communication).

Throughout its range Coulter pine usually grows on the drier, warmer and rockier sites, but it may sometimes be found on the moister, cooler and more fertile ones. It is quite versatile in its ecological requirements and in the number and kind of plant associations in which it is found. Coulter pine grows intermixed with various oak species (except at the Idria locality) and is found associated with Jeffrey pine in all areas studied with the exception of the three northernmost populations of Mount Diablo, Mount Hamilton, and Fremont's Peak (Zobel, 1952). In addition, it is associated with ponderosa pine, sugar pine, coast redwood, Santa Lucia fir, incense cedar and white fir in various combinations at the other areas studied. For example, in the Northern Santa Lucia Mountains all species listed but white fir and incense cedar are found while to the south, at Black Mountain, coast redwood and Santa Lucia fir are replaced by incense cedar and white fir.

Despite the varied ecological and geographical conditions which prevailed in the nine isolated populations, a remarkable similarity was found for most of the characters studied. Although these were chosen primarily for their suitability in analyzing the Coulter-Jeffrey hybrid, they also included those characters most important in determining variation within the two parental species. Characters studied can be broadly grouped into four classes which include those of cone, foliage, oleoresins (volatiles only), and seed.

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Table 1. Areas Where Coulter Pine Was Studied in California

Key to Localities	Area	County	Mean annual diam. growth inches	Elevation feet
DC	Mount Diablo** (Mitchell Canyon)	Contra Costa	.28	500
MH	Mount Hamilton (Isabel Valley Ranch)	Santa Clara	.26	4,000
FP	Fremont's Peak** (Fremont's Peak State Park)	San Benito	.40	3,000
CR	Chew's Ridge* (Los Padres National Forest)	Monterey	.55	5,000
I	Idria** (Clear Creek)	San Benito	.18	3,500
AM	Alvin Meadow* (San Bernardino National Forest)	Riverside	.38	5,000
BM	Black Mountain (San Bernardino National Forest)	Riverside	.30	7,000
LM	Laguna Mountain (Cleveland National Forest)	San Diego	.37	6,000
BR	Benton's Ranch (Corta Madera Valley)	San Diego	.27	4,200

From four to fifteen trees were sampled at each area.
*Trees well-formed.
**Trees with poor form.

Three cone characteristics were analyzed. Specific gravity of the cones was simply determined and found to be very constant in all 9 areas, the weighted average being 0.93. This means that the cones barely float in water. Cone size was also studied, but proved to be rather variable, absolute lengths and widths varying greatly from site to site (length varied from approximately 10 cm. to over 30 cm., while variation in width was equally large). The ratio of length to width was found to be relatively constant, the average being 1.6 (range 1.4 to 1.7). The third cone character used was qualitative and consisted of a study of several morphological features such as the position and form of the umbo and apophysis, and color of the cone. Disregarding size differences, all these cone characters were

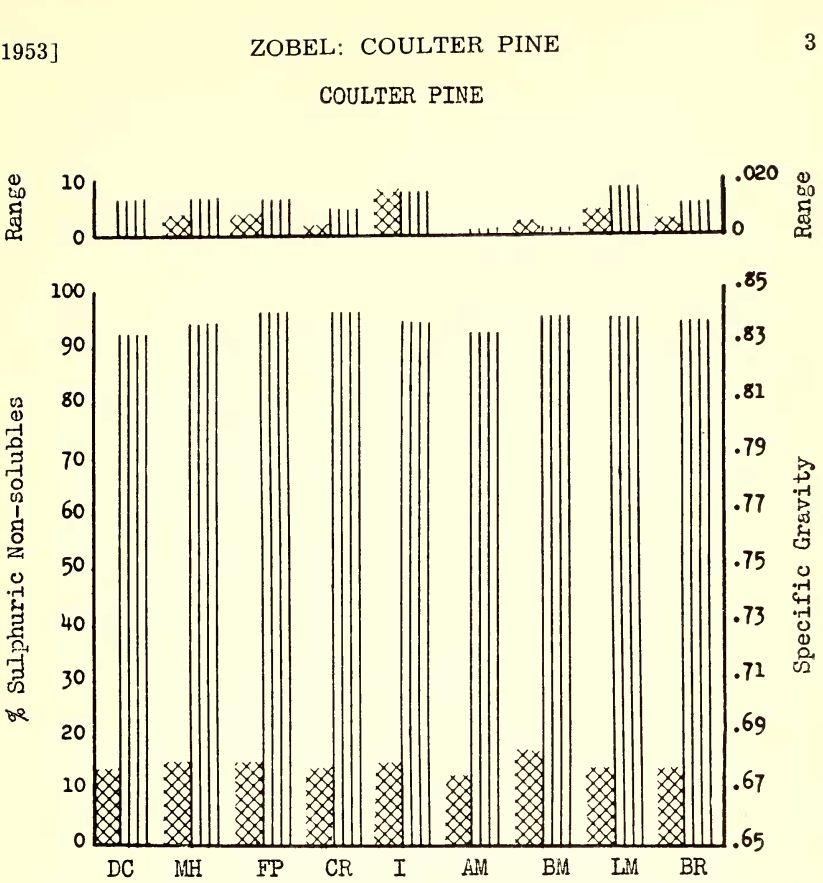

FIG. 1. Graph showing the percent sulphuric acid non-solubles and specific gravities of the steam volatiles of the oleoresins from trees in the nine Coulter pine populations (see Table 1 for key to localities). The cross-hatched area represents the surphuric acid non-solubles and the area of vertical lines represents specific gravities. Note the uniformity among the populations. Range indicates range of variation within populations.

relatively constant throughout the range, with the exception of the Idria locality, as noted later.

Six characteristics of foliage were studied, only one of which was quantitative. These were all originally chosen for their sharp contrast to Jeffrey pine. Anatomically, it was found that a cross section through the needle showed a V-shaped stomata and endodermis with thin walls in all populations studied. Surface stomata shape was rectangular with no wax connections. Number of lines of stomata on the ventral surface varied considerably from tree to tree within each population, but population averages varied from 12 to 16 rows, average slightly over 13. Also evaluated was needle flexibility and the four bud characters of color (brown), presence of resin droplets, non-reflexed scales, and sharp point. The bud characters

were very constant everywhere, although needle flexibility varied somewhat with vigor of tree.

Seed characters studied were ratio of wing length to seed length and seed coat thickness. Seed coat thickness was remarkably uniform in all populations averaging .032 inch, with population averages varying only .028 to .035. Wing length to seed length ratio averaged 1.7, populations varying from 1.4 to 1.9. Although seed color and size were not used, considerable variation between populations was noted, and Fielding (1949) uses these characters as an indication of the beginning of racial variation within certain populations.

The volatile portion of the oleoresins was analysed quantitatively. All characters but optical rotation were very uniform throughout Coulter pine's range. Variability in optical rotation was not unexpected. It averaged —18 degrees, while index of refraction average 1.471, specific gravity .839 and sulphuric acid non-solubles was 21 per cent. Two of these characters are shown in fig. 1 and illustrate the constancy among populations. A brief statistical analysis of oleoresin and cone specific gravities showed that the samples from the nine areas were so similar that they might all have been obtained from the same population.

The general concept of the role of isolation as expressed by Dobzhansky (1941) and Stebbins (1950) would lead us to believe that a number of geographic races should have evolved in the widely separated Coulter pine populations. On the basis of the characters used in this study, however, it appears that such definite local races have not yet evolved, a fact that may be explained partially by the relatively short time, in a geological sense, that these nine populations have been isolated from one another. Undoubtedly fire and man's activities have determined in part the present isolated pattern of distribution of Coulter pine. Sudworth (1908), in discussing the presence of this pine on Fremont's Peak (San Benito County), mentions that it was formerly found over the whole summit of the Gabilan Range. At the present time the population is restricted to Fremont's Peak proper and a few other high areas, with no indication that it has been part of a more extensive stand. When the period of time necessary for one gèneration of trees to mature and reproduce is taken into account, it is highly improbable that by now the Fremont population would show any effects of isolation.

There is, however, a tendency towards the initiation of distinct geographic races in some populations. This tendency is especially pronounced in the notably different population found near Idria, San Benito County where cones are much smaller than the average, and the shape and size of the umbo and apophysis are extremely variable. On some trees the cones have short, hooked spines while others have long-attenuate,

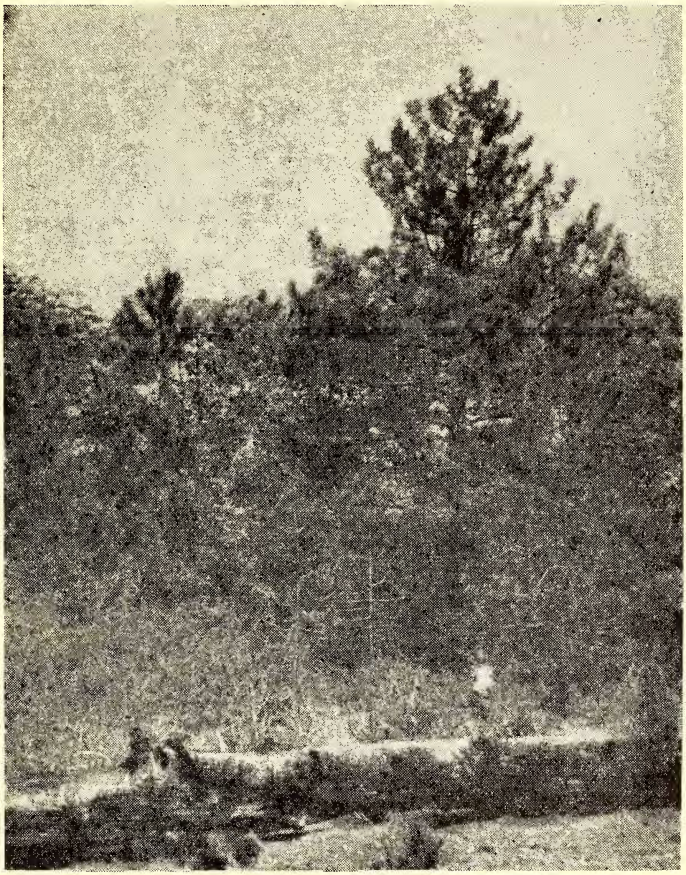

FIG. 2. The common limby form of Coulter Pine, often considered to be the only form the tree attains. Compare with fig. 3.

hooked or even straight spines. Most likely the Idria population represents an edaphic-climatic ecotype in the formative stage, since this is a region where very hot summers, low annual rainfall and poor serpentine, sandy and alkaline soils prevail.

Lemmon (1902) proposed that the Coulter pines in Mitchell Canyon on Mount Diablo be designated *P. Coulteri* var. *Diabloensis* on the basis of their being smaller trees and having shorter leaves, smaller cones, and larger seeds than the type. Cones from the Mitchell Canyon area collected during the course of this study, however, proved to be slightly longer than the average for all nine populations, needle length was average, and seed size was identical with that of seed from Chew's Ridge and Fremont's Peak. Seed weight, as reported by Fielding (1949) was also average. Fielding also stated that cone

FIG. 3. The large tree on the right shows the fine form that Coulter pine sometimes attains. This tree is growing on a good site in mixture with Jeffrey pine at Alvin Meadow. Less than a mile distant is a pure stand of Coulter pine with a form similar to the trees shown in fig. 2 (see Table 1 for key to areas).

length of the Mount Diablo trees exceeded that in the other localities studied. Therefore, in the writer's opinion, most characters of the Mount Diablo (Mitchell Canyon) Coulter pine fall within the normal range of variation, and subspecific status is not warranted. The writer agrees with Lemmon that the trees in this area are more branched and have poorer form than those of many other Coulter pine populations.

Coulter pines do not all have the same general form (i.e., numerous long, coarse, sweeping limbs that nearly touch the ground) even though their cones, oleoresins, foliage, and seeds are similar (fig. 2). Occasionally, stands of small area were found, usually on more favorable sites, where the Coulter pines

were tall, straight and small-limbed (fig. 3). Whether these well-formed trees are merely the result of similar genotypes selected by superior habitats, or whether they are the result of past introgression of genes of the well-formed Jeffrey pine into Coulter pine, must await suitable genetic tests. Regardless of cause, Coulter pine frequently has the form of a good timber tree which should interest foresters when considered along with its rapid growth rate. In the regions studied, the best-formed trees were found at Chew's Ridge in Monterey County and at Alvin Meadow in Riverside County, while the poorer formed trees were found on Mount Diablo in Contra Costa County, and Fremont's Peak and Idria in San Benito County. However, the populations having the faster diameter growth do not necessarily have the better tree form (Table 1).

Based on the apparent ease of reproduction and the predominance of Coulter pine seedlings over those of its companion species when growing in mixed stands, Coulter pine would appear to be a potentially expanding species. Barring repeated fire on chaparral covered slopes, young Coulter pines become established and dominate an area in a short time if left undisturbed.

Coulter pine has an unfortunate reputation in the literature as a scrubby, inferior, much branched and generally undesirable tree. This is a result of its ability to grow on extremely poor sites where it has poor form and is conspicuous because no other conifers are found growing with it. However, on favorable sites it frequently makes a fine tree. Genetic studies to determine the best genotypes should enable Coulter pine to be included as a regular member of our "wood producing" conifers, either as the species or as a hybrid with some related species such as Jeffrey pine.

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